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CRAB SHELL-CRUSHING PREDATION AND GASTROPOD ARCHITECTURAL DEFENSE

MARK D. BERTNESS
Division of Biology and Medicine, Box G, Brown University, Providence, RI 02912, U.S.A.

and

CLIFFORD CUNNINGHAM
Biology Department, Yale University, New Haven, CT 06511, U.S.A.

Abstract: The shell-breaking behavior of the crabs *Ozius verreauxii* Saussure 1853 and *Eriphia squamata*, Stimpson 1859 from the Bay of Panama is described. The master claws of both these crabs are well designed for breaking shells. Small shells, relative to the size of a crab predator, are crushed by progressively breaking off larger segments of a shell's apex, while larger shells are peeled by inserting a large dactyl molar into the aperture of a shell and progressively chipping away the lip of the shell.

Heavy gastropod shells are shown to be less vulnerable to crab predators than lighter shells, and narrow shell apertures and axial shell sculpture are demonstrated to be architectural features that deter crab predation. The incidence of architectural features which deter crab predation appears to be higher for smaller gastropod species than for larger gastropods which are too large for most crab predators. Large fish predators prey upon both gastropods and shell-crushing crabs. To avoid fish predators, both these prey groups seek refuge under rocks when covered by the tide. Fish predation thus appears to enforce a close sympatry between smaller gastropods and their crab predators.

INTRODUCTION

Shell-crushing predation by decapod crustaceans has been shown to be an important process in the evolution of shell (Kitching & Lockwood, 1974; Vermeij, 1976, 1977, 1978; Zipser & Vermeij, 1978) and crab claw design (Shoup, 1968; Vermeij, 1977). This coevolutionary relationship has been shown to vary latitudinally with heavier predation pressure by crabs in tropical latitudes (Vermeij, 1977, 1978), leading to heavier shells and shell armor in tropical gastropods (see Vermeij, 1978, for review). In addition, it has been suggested that interpopulation variation in the shell thickness of direct-developing littoral gastropods is correlated with the occurrence of predatory crabs, such that individuals in populations subject to heavy predation have thicker shells than conspecifics from populations where predation is not as severe (Bertness, 1977; Kitching & Lockwood, 1974).

Teleost fish such as the spiny puffer fish (*Diodon* spp.) and smooth puffer fish (*Arothron* spp.) also prey upon shelled organisms by crushing them in their strong mouthparts or pharyngeal mills (Vermeij, 1978; Palmer, 1979). Palmer (1979) has shown that spines on some gastropod shells protect them from teleost predators and demonstrated that the occurrence both of shell-crushing fish and spinose shell sculpture increases from temperate to tropical seas. In the Bay of Panama, predation by teleost fish on littoral gastropods left exposed on open rock surfaces during high tide has been experimentally shown to be as high as 28% every 24-h tidal cycle (Bertness, 1980c). To cope with this extremely high predation pressure, littoral gastropods in the Bay of Panama and other tropical areas seek refuge under rocks or in fissures during high tide or avoid being covered by the incoming tide by always staying immediately above the water (pers. obs.).

All shell architectural modifications used to escape from teleost predators appear to be related to reaching a size too large to be handled by fish. With the exception of extremely thick and heavy-shelled gastropod species, e.g. *Thais melones*, *Diodon* spp., are capable of crushing any shell that they are able to fit into their crushing mouthparts (unpubl. data). All littoral rocky shore gastropods that forage in the open in the Bay of Panama exposed to teleost predators are either large individuals that have escaped the brunt of fish predation because of their large size or are species that have spinose shell architecture which effectively increases their external dimensions (Palmer, 1979). Shell architectural features which appear to deter crab predators of gastropods are common in smaller snail species. Such features include narrow apertures, short spires, and axial ribbing (Vermeij, 1978), all features which have been postulated to hamper the effective handling of gastropod shells by the crushing claws of crab predators. These smaller gastropod species avoid fish predation by retreating to cryptic habitats during high tide (unpubl. data).

In this paper the shell-breaking behavior of two tropical Eastern Pacific intertidal crabs on the most commonly available gastropod prey in their natural environment is examined. We describe different shell-crushing behaviors and the functional morphology of the crushing claws of the predators. Then we examine the vulnerability to predation of the sympatric gastropod species as a function of shell architectural form and the investment in shell material as a defensive measure. Finally, we examine the frequency of shell damage in shells worn by hermit crabs in the Bay of Panama to assess the success of shell architectural defensive measures in these gastropods.

METHODS

The predatory crabs *Eriphia squamata* Stimpson 1859, and *Ozius verreauxii* Saussure 1853, were collected in rocky intertidal areas near the Smithsonian Tropical Research Institute Naos Marine Laboratory in the Bay of Panama from June to August 1978. Each crab was maintained in a separate shaded aquarium and its water was changed daily. To determine the largest shell each individual crab was capable of crushing for each of several gastropod species (critical size, sensu Vermeij, 1976), a wide size range of five to eight freshly collected shells occupied by hermit crabs was introduced to each predator. Hermit crab occupied shells were used to standardize the availability of each shell type to the predators and to avoid the potential effects of differential gastropod behavior and palatability on the laboratory results. On each of the following 7 days or when no predation had been observed in 2 days, broken shells were removed and examined, and either all shells smaller than those broken were removed, or larger shells were added if the predator had broken the largest shell offered. Each individual predator/shell species size refuge determination required from 7 to 14 days to complete. Only shells which had no previous injuries or encrustations were used to avoid the influence of these variables on a shell's vulnerability to predation. Each shell offered to the predators was measured to 0.1 mm with vernier calipers using columellar length as a size standard for all gastropod species examined except *Nerita funiculata*. With *N. funiculata*, aperture width was found to be a more reliable, replicable measure. During these tests, observations were also made on the feeding behavior of the crabs.

In order to examine the critical shell sizes among shells that differ in shape, allometric relationships were determined for each gastropod species examined to convert the shell length measurements determined in the size refuge tests into shell weights and gastropod tissue weights. For each gastropod species, a wide size range of 20 to 30 individuals was collected and measured. The snails were then boiled and their tissues removed with forceps. The tissues and shells were then dried at 100 °C for 12 h and weighed to 0.001 g on an analytical balance.

To experimentally test the antipredation value of the large terminal axial varices of *Cantharus ringens*, size refuge tests were made with laboratory predators given both shells from which the varices had been artificially removed and normal (control) shells. The varices of experimental shells were removed with a grinding wheel to form a uniformly smooth-surfaced shell. Microscopic examination of the ground edge of altered shells indicated that the structure of the remaining shell material was not altered and that there was no structural difference between the removed and remaining shell material.

Predator preference for gastropod or hermit crab occupied shells was determined by offering predators size-matched shells with either hermit crab or gastropod occupants. To prevent the gastropods from avoiding predators by moving above the water in the aquaria, the water level was kept at 5 cm and the inside wall of the aquaria was coated with an adhesive (Tanglefoot) at the water's edge. To examine the influence of hermit crab occupation on the predation size refuge of a shell, critical size determinations were made on live *Acanthina brevidentata*, using the same experimental procedures and predators that had been used to determine the size refuge for *Acanthina* shells occupied by hermit crabs.

Field collections of hermit crab occupied shells were made at Culebra and Flamenco Islands, Panama and examined for the incidence of identifiable predator damage (see Bertness 1980a for the sampling methods used and for a description of the study areas). Shells which were badly eroded or encrusted with epiphytes could not be reasonably scored for injury and were not included in the final data analysis.

THE SPECIES

The crabs used in the laboratory predation tests, *Ozius verreauxii* and *Eriphia squamata*, are the two most common shell-crushing intertidal crabs in the Bay of Panama (pers. obs.). Throughout the remaining text these two species will be referred to by their generic names. *Ozius*, a relatively large crab reaching sizes of

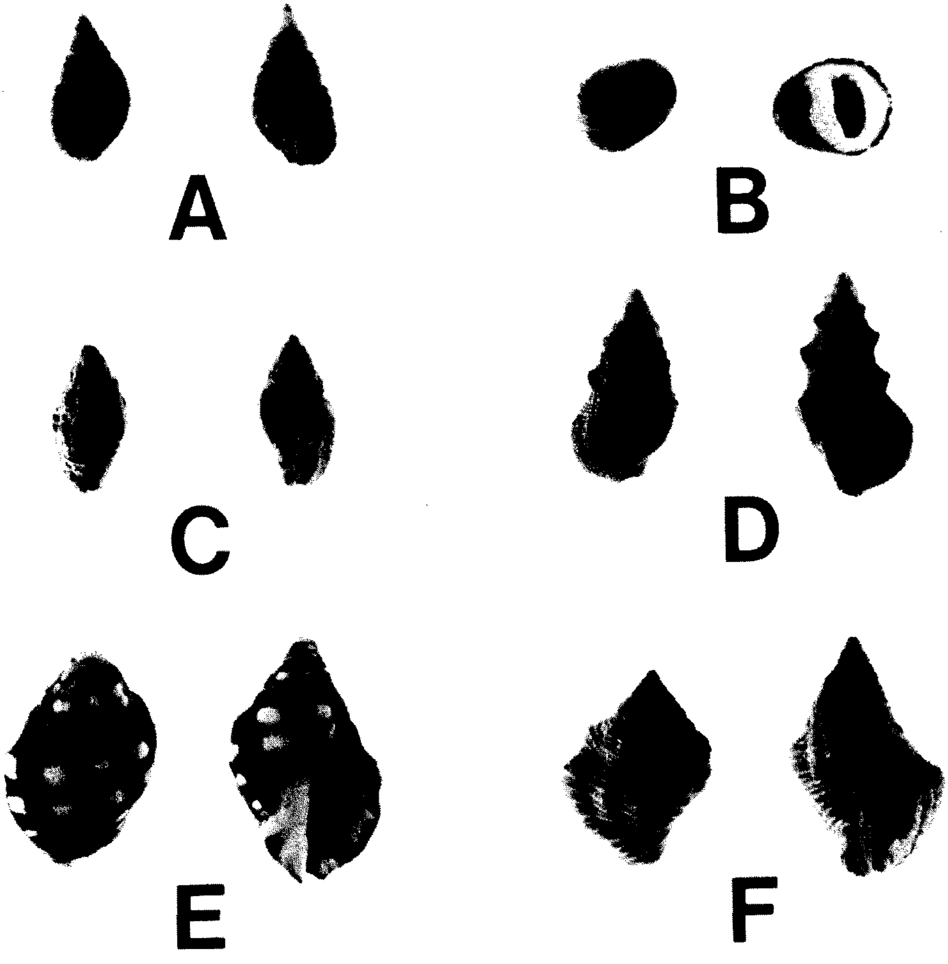

Fig. 1. Shells of gastropod species used in the predation size refuge determinations: A, *Planaxis planicostata*; B, *Nerita funiculata*; C, *Anachis fluctuata*; D, *Cerithium stercusmuscarum*; E, *Acanthina brevidentata*; F, *Cantharus ringens*.

81.7 mm carapace width (Rathbun, 1930), is generally found in groups of 2 to 10 individuals under rocks at tidal levels from + 1 m to − 1 m. It is a docile crab that does not react aggressively to being handled and was never observed to act aggressively to conspecifics in the field or laboratory. Groups of *Ozius* are routinely found under the same rocks where shell fragments accumulate from their predatory behavior. Observations of the foraging behavior of *Ozius* reveal that it commonly moves up and down in the splash zone in the vicinity of its burrow, but retreats to its burrow during daytime low and high tides. *Eriphia*, a smaller xanthid reaching a maximum size of 51.3 mm carapace width (Rathbun, 1930), is an extremely aggressive and solitary crab which resides in fissures and under rocks at low tide and when covered completely by high tide. *Eriphia* are often seen interacting aggressively in their natural environment, apparently disputing the ownership of burrows. When two *Eriphia* are placed together in a small aquarium, the smaller of the crabs inevitably loses its master claw in aggressive interactions. *Eriphia* are found from + 1 m to 0 m in the intertidal region and are found actively foraging when the tide is changing and particularly during evening low tide exposures. Since *Eriphia* are not found predictably in the same location from day to day, they do not appear to defend a permanent burrow.

The gastropod species examined in this study are illustrated in Fig. 1. They are some of the most common and abundant gastropods on rocky intertidal shores in the Bay of Panama and represent a wide range of architectural types. All forage only during evening low tide exposure and when the tide is changing over their habitat; during daytime low tides and when covered by the tide, these snails are inactive under rocks and in crevices (pers. obs.).

RESULTS

SHELL PREDATION BEHAVIOR

Both *Eriphia* and *Ozius* were observed handling and breaking shells in the laboratory. Shell-breaking behaviors were found to be very predictable and did not differ noticeably between the two species. The following description, therefore, applies to both.

When presented with a group of shells, these crabs will generally move one to four shells under their body, restraining them by forming a cage with their walking legs. Hermit crabs that attempted to escape were usually restrained by the predator. Using their walking legs, the predator then moves one of the shells forward and grasps it with the minor claw, which transports the shell to the mouthparts. At this point, the crab rotates the shell around its axis using the minor claw and mouthparts. While rotating the shell, the crab will frequently pause and examine the aperture area of the shell and any shell relief with its mouthparts. Then the shell is transferred from the crab's minor claw to its master claw. Shell breakage by the master claw in these two xanthid species is accomplished by one of two different techniques, depending on the relative size of the shell compared to the predator. The first method, crushing (Zipser & Vermeij, 1978), is used successfully on shells that are small relative to the size of the crab predator. Peeling (Shoup, 1968) is used on larger shells close to the largest sized shell a particular crab is able to break (critical size, sensu Vermeij, 1976). Generally, when initially examining a shell the predator will hold the shell in a crushing position and if the shell is too large for the crushing technique to be successful, the crab will reposition its hold on the shell to a peeling grasp. When handling extremely large shells, both crab

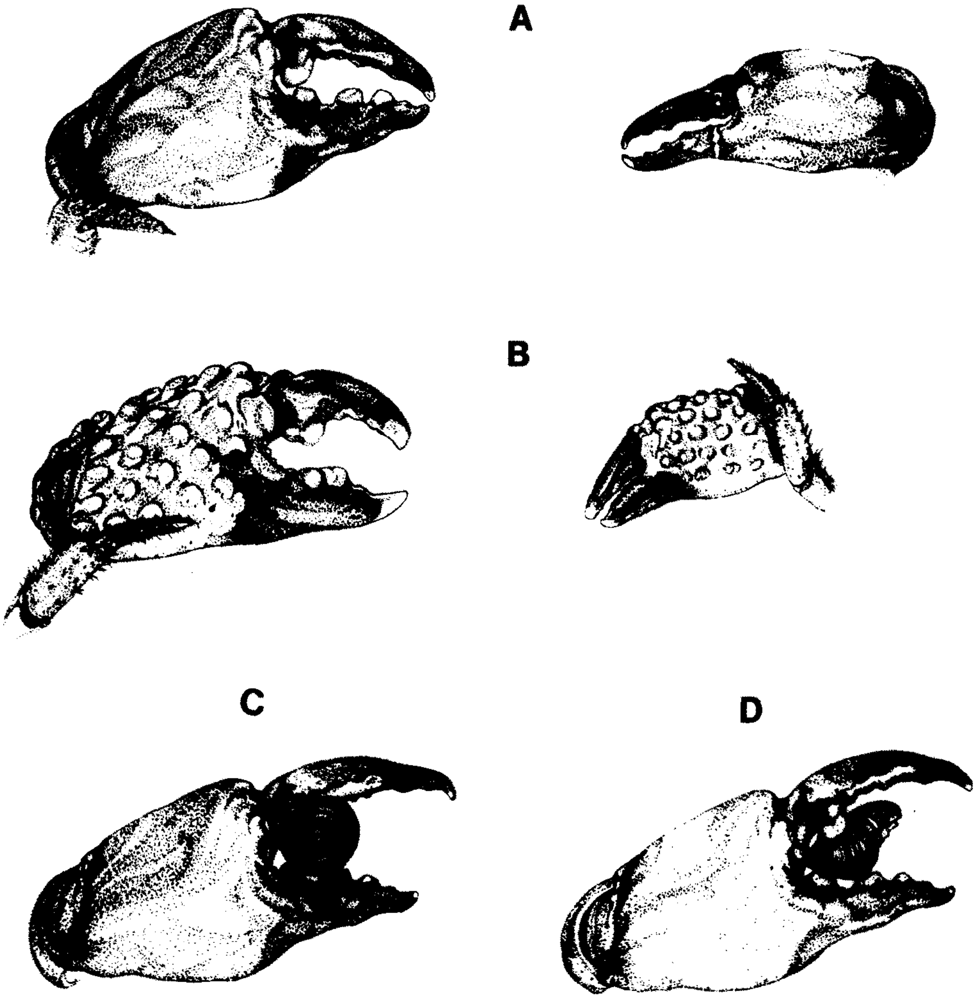

Fig. 2. Master (left) and minor (right) claws of *Ozius verreauxii* (A) and *Eriphia squamata* (B) and the master claw of *O. verreauxii* in a shell-peeling hold (C) and shell-crushing hold (D). (Drawings by Marisal Pastor.)

species will directly hold the shell in the peeling position, foregoing any attempt to employ the crushing technique.

In breaking a shell using the crushing technique, a crab holds the shell in its master claw so that the apex of the shell rests between the dactylus and fixed finger of the claw (Fig. 2D). Molariform teeth on the fixed finger and one large tooth on the dactylus hold the shell securely in the claw in a position which maximizes mechanical advantage. The claws of *Ozius* and *Eriphia* are illustrated in Fig. 2A and B respectively, showing the structure and position of the claw teeth. Once the shell is positioned in the crushing hold (Fig. 2D), the apex of the shell is severed and the shell is then repositioned in an identical manner above the broken apex. This process continues until the shell is sufficiently broken for the predator to remove the occupant of the shell or the size and/or strength of the shell prevents further breakage. If the shell is too large to be broken by the crushing technique the predator generally will reposition the shell and attempt to use the peeling technique.

In peeling, the shell is positioned in the claw so that the large proximal molar of the dactylus is inserted into the aperture of the shell, resting on the shell lip, with the body of the shell held firmly in place by the curvature and indention of the fixed finger (Fig. 2C). Pressure is then applied by the dactylus until the shell lip fractures. The shell is then repositioned in the same fashion above the broken lip and the process is repeated until the shell is peeled back sufficiently to remove the shell's resident. This shell breaking technique has been described by Shoup (1968) for *Calappa* spp. The angle of attack a crab takes in using the peeling technique varies depending on the relative size of the shell. With relatively small shells peeling is performed with the master claws at a 90° angle to the axis of the shell. For larger shells, close to the largest size a particular crab is capable of breaking, the circumference of the shell prevents a 90° angle of attack, so larger shells are attacked more diagonally.

A third type of shell breaking behavior was used by *Eriphia* and *Ozius* only on the shells of *Nerita funiculata*. Nerite shells have a distinctive architecture in comparison to the other five shell-types tested (Fig. 1). They have an extremely short spire and a unique internal shell structure since they resorb old whorls as they grow (Vermeij, 1978). Externally, the nerite shell has the appearance of a half-sphere, since its body almost entirely consists of a terminal whorl and its columella is a thin shelf on the flat ventral surface. Both *Ozius* and *Eriphia* appeared to have difficulty employing the shell crushing technique on nerite shells. When shell crushing was attempted on nerite shells, the entire shell body was grasped in a shell-crushing hold and the shell was crushed in one act, rather than the progressive crushing of larger and larger segments of the apex, as observed with all other shells tested (Fig. 1). Shell peeling also did not appear to be an effective shell breaking technique with nerite shells, since shell width exceeds shell length (Fig. 1). When predators were observed attempting to peel a nerite, they were found with their dactyl molar inserted in the aperture near the columella, rather than in the area of the aperture furthest from the columella, as was observed in the peeling of all other shell-types tested. Three out of the 11 *Ozius* and 4 of the 12 *Eriphia* examined in the laboratory utilized a novel technique of breaking *Nerita funiculata* shells. After examining a nerite shell, the crab predator would insert the fixed finger of the master claw into the aperture of the shell under the columella. Then, by applying pressure with the dactylus on the exterior of the columella, it would break out the shelf of the shell and remove the shell's occupant. None of the laboratory predators employed this shell breaking technique on their first laboratory contact with a nerite, but predators that used this technique continued to break nerite shells in this manner throughout the remaining tests. This implies that this technique may be a learned method. This method appears to occur in nature since nerite shells with their shelves removed are found in the field.

The removal of hermit crabs from their shells without shell breakage was seen only with hermit crabs occupying *Nerita funiculata* shells. This appeared to be due to the relatively large aperture of *N. funiculata* in comparison to the other shell-types examined (Fig. 1). Extraction of hermit crabs was observed with 6 of 11 *Ozius* and 4 of 13 *Eriphia* predators on nerite-shelled crabs. As with the shell breaking of nerite shells, the laboratory predators that extracted hermit crabs all repeated this technique once it was initially observed. To extract hermit crabs from their shells, the predators would insert their narrow minor claw (Fig. 2) into the aperture of the shell and simply grab the crab and pull it out.

SHELL-TYPE PREDATION SIZE REFUGES

Results from the critical shell size determinations with smaller gastropod species and *Ozius* and *Eriphia* predators are shown in Tables I and II respectively. The data are presented giving the largest shell broken by the shell-crushing and peeling

TABLE I

Results of gastropod species predation size refuge determinations with *Eriphia squamata* predators: all shells had hermit crab occupants.

Predator and prey	Largest crushed (mm)	Largest peeled (mm)	Smallest uneaten (mm)	Shell weight of largest taken (g)	Flesh weight of largest taken (g)
32.4 mm male*					
Anachis fluctuata	14.7	–	15.5	0.40	0.020
Planaxis planicostata	17.7	–	18.2	0.90	0.028
Cerithium stercusmuscarum	17.5	24.6	25.5	1.28	0.262
Nerita funiculata	14.5	–	15.3	5.49	1.395
28.5 mm male*					
Anachis fluctuata	16.0	–	16.7	0.49	0.024
Planaxis planicostata	–	17.8	18.0	0.91	0.028
Cerithium stercusmuscarum	–	23.0	26.0	1.29	0.263
Nerita funiculata	10.8	12.5	12.8	5.12	1.123

TABLE I (continued)

Predator and prey	Largest crushed (mm)	Largest peeled (mm)	Smallest uneaten (mm)	Shell weight of largest taken (g)	Flesh weight of largest taken (g)
21.7 mm male*					
Anachis fluctuata	13.3		13.7	0.30	0.015
Planaxis planicostata	13.5	–	14.1	0.40	0.012
Cerithium stercusmuscarum	–	19.5	20.7	0.78	0.225
Nerita funiculata	–	10.5	13.3	3.40	0.992
33.8 mm male*					
Anachis fluctuata	14.5	15.3	16.5	0.39	0.022
Planaxis planicostata	–	15.4	16.0	0.64	0.019
Cerithium stercusmuscarum	21.6	24.5	25.6	1.27	0.261
Nerita funiculata	14.2	–	16.7	5.45	1.364
32.1 mm male					
Anachis fluctuata	15.4	–	16.5	0.45	0.022
Planaxis planicostata	–	19.6	20.1	1.09	0.035
Cerithium stercusmuscarum	21.6	25.3	–	1.34	0.267
Nerita funiculata	15.0	15.5	16.3	5.55	1.445
28.8 mm female*					
Anachis fluctuata	16.1	–	16.5	0.49	0.024
Planaxis planicostata	–	16.3	17.1	0.84	0.023
Cerithium stercusmuscarum	–	24.1	25.2	1.23	0.258
Nerita funiculata	–	12.8	15.2	5.27	1.224
25.1 mm female*					
Anachis fluctuata	11.3	–	12.4	0.13	0.009
Planaxis planicostata	–	13.2	13.9	0.36	0.011
Cerithium stercusmuscarum	–	19.2	19.7	0.75	0.222
Nerita funiculata	–	11.0	11.5	3.48	1.043
27.5 mm male*					
Anachis fluctuata	13.2	–	14.5	0.33	0.017
Planaxis planicostata	10.55	13.5	14.0	0.40	0.015
Cerithium stercusmuscarum	–	24.3	24.7	1.25	0.260
Nerita funiculata	–	12.0	12.5	5.12	1.123
35.2 mm male					
Anachis fluctuata	–	17.0	–	0.55	0.027
Planaxis planicostata	-	22.0	–	1.30	0.045
Cerithium stercusmuscarum	–	23.8	24.6	1.21	0.256
Nerita funiculata	15.9	–	17.3	5.65	1.536
31.3 mm male					
Anachis fluctuata	15.0	16.1	17.8	0.43	0.024
Planaxis planicostata	12.7	17.3	18.7	0.86	0.009
Cerithium stercusmuscarum	–	24.7	–	1.29	0.263
34.4 mm female					
Anachis fluctuata	16.5	16.2	–	0.50	0.0247
Planaxis planicostata	–	22.0	–	1.30	0.045
Cerithium stercusmuscarum	20.0	22.2	23.3	1.06	0.245

* Size refuge attained by all four snail species tested.

TABLE II

Results of gastropod species size refuge determinations with *Ozius verreauxii* predators: all shells had hermit crab occupants.

Predator and prey	Largest crushed (mm)	Largest peeled (mm)	Smallest uneaten (mm)	Shell weight of largest taken (g)	Flesh weight of largest taken (g)
36.1 mm male					
Anachis fluctuata	15.7	–	16.3	0.47	0.023
Planaxis planicostata	–	15.9	16.2	0.67	0.020
Cerithium stercusmuscarum	17.0	24.7	–	1.29	0.263
Nerita funiculata	15.7	–	17.7	5.63	1.516
33.8 mm female*					
Anachis fluctuata	16.1	–	16.7	0.49	0.024
Planaxis planicostata	12.0	17.7	18.2	0.90	0.028
Cerithium stercusmuscarum	16.5	24.5	27.0	1.27	0.261
Nerita funiculata	13.5	–	15.9	5.18	1.164
51.1 mm male					
Anachis fluctuata	17.5	–	–	0.58	0.028
Planaxis planicostata	-	18.1	19.5	0.95	0.030
Cerithium stercusmuscarum	17.4	27.2		1.49	0.281
Nerita scabricostata	20.5	–	21.8	6.10	2.000
36.1 mm male					
Anachis fluctuata	14.5	15.7	16.3	0.47	0.023
Planaxis planicostata	14.6	18.0	19.1	0.95	0.030
Cerithium stercusmuscarum	17.0	24.7	–	1.29	0.263
Nerita funiculata	13.7		14.7	5.39	1.315
53.5 mm female					
Anachis fluctuata	16.7	–		0.53	0.026
Planaxis planicostata	19.4	22.5	–	1.35	0.047
Cerithium stercusmuscarum	19.3	25.3	–	1.34	0.267
Nerita scabricostata	18.8	21.5	24.0	5.95	2.101
40.0 mm female					
Anachis fluctuata	17.7	–	–	0.59	0.029
Planaxis planicostata	15.5	19.3	19.9	1.06	0.034
Cerithium stercusmuscarum	20.0	24.3	–	1.25	0.260
Nerita funiculata	13.5	–	15.1	5.36	1.294
41.5 mm female					
Anachis fluctuata	18.0	–	–	0.61	0.030
Planaxis planicostata	16.0	20.5	21.2	1.17	0.039
Cerithium stercusmuscarum	19.2	24.3	–	1.25	0.260
Nerita funiculata	13.2	–	16.0	5.32	1.264
33.8 mm female					
Anachis fluctuata	16.1	–	16.7	0.49	0.024
Planaxis planicostata	12.0	17.7	18.9	0.90	0.028
Cerithium stercusmuscarum	16.5	24.5	–	1.27	0.262
Nerita funiculata	12.2	14.5	14.9	5.18	1.395

TABLE II (continued)

Predator and prey	Largest crushed (mm)	Largest peeled (mm)	Smallest uneaten (mm)	Shell weight of largest taken (g)	Flesh weight of largest taken (g)
67.0 mm female					
Planaxis planicostata	20.8	22.4		1.34	0.046
Cerithium stercusmuscarum	23.5	27.2		1.49	0.281
Nerita scabricostata	18.8	22.3	23.2	5.95	1.828
42.6 mm male					
Planaxis planicostata	14.2	20.2	20.8	1.15	0.038
Cerithium stercusmuscarum	18.0	25.1	–	1.32	0.266
59.4 mm female					
Planaxis planicostata	–	20.4	21.3	1.16	0.039
Cerithium stercusmuscarum	20.4	25.8		1.38	0.271
Nerita scabricostata	23.5		24.0	6.34	2.301
46.2 mm male					
Planaxis planicostata	–	20.1	20.5	1.14	0.037
Cerithium stercusmuscarum	21.7	24.9	–	1.31	0.265
36.7 mm male					
Anachis fluctuata	16.4		–	0.52	0.0253
Planaxis planicostata	14.6	18.1	18.75	0.95	0.030
Cerithium stercusmuscarum	20.9	23.7		1.20	0.256
Nerita funiculata	17.7	–	18.8	5.84	1.717
48.8 mm female					
Anachis fluctuata	17.1	–	–	0.56	0.028
Planaxis planicostata	–	20.5	21.0	1.17	0.039
Cerithium stercusmuscarum	22.6	26.0	–	1.39	0.273
Nerita scabriscostata	18.0	–	21.0	5.87	1.747

* Size refuge attained by all four snail species tested.

techniques on a shell length basis. Using shell length/shell weight and shell length/flesh weight allometric relationships for the gastropod species (Tables III and IV), the shell and flesh weights of the absolute critical size for each predator and gastropod species tested are also given. When a predator was able to break the largest shell available, critical size was considered to be undetermined for comparative purposes, since this indicated that no size refuge from predation was attained by a given shell-type with the test predator.

For both *Ozius* and *Eriphia* predators the critical size for peeled prey is significantly larger than for crushed prey (*Ozius* $n = 29$, $P < 0.001$, paired t-test; *Eriphia* $n = 11$, $P < 0.01$, paired t-test), considering only predators which revealed both crushing and peeling critical sizes. This verifies the direct observation that crushing predation is used on smaller shells, while with larger shells the peeling technique is employed.

To make interspecific comparisons of the effectiveness of different shell architectural types as a defense against predation, any outside shell dimension is inadequate. This is due to differences among gastropod species in shell shape, thickness, ornamentation, and internal reinforcement (Bertness, 1980b). Interspecific comparisons among the vulnerability of different gastropod species to predators can be made by examining critical size shell or flesh weights. In this way different gastropod species can be compared assuming that at equivalent shell or flesh weights the snails have invested equally in shell construction as an antipredation investment. In making these interspecific comparisons from the data presented in Tables I and II, only predators which did not take the largest of any of the shell species offered can be used (8 cases). Both shell weight and flesh weight critical size comparisons indicate that predation resistance decreases in the order *Anachis fluctuata* > *Planaxis planicostata* > *Cerithium stercusmuscarum* > *Nerita funiculata* ($P < 0.05$, paired t-test, all pairs tested separately). If these four gastropod species are compared in terms of shell weight investment per unit of flesh weight (unpublished data), shell investment decreases in a similar manner with *Planaxis planicostata* > *Anachis fluctuata* > *Cerithium stercusmuscarum* > *Nerita funiculata*, with only *Planaxis planicostata* and *Anachis fluctuata* reversed in the order. This

TABLE III

Regression equations used to estimate dry flesh weight (Y) in grams from gastropod shell length (X) in millimeters.

Gastropod species	n	Regression equation	r^2
Cantharus ringens	24	$Y = -0.131 + 0.009X$	0.91
Planaxis planicostata	24	$Y = -0.039 + 0.004X$	0.90
Acanthina brevidentata	29	$Y = -0.238 + 0.016X$	0.88
Cerithium stercusmuscarum	30	$Y = -0.083 + 0.007X$	0.86
Anachis fluctuata	26	$Y = -0.025 + 0.003X$	0.88
Nerita funiculata	37	$Y = -0.065 + 0.101X$	0.91

TABLE IV

Regression equations used to estimate dry shell weight (Y) in grams from gastropod shell lengths (X) in millimeters.

Gastropod species	n	Regression equation	r^2
Cantharus ringens	24	$Y = -12.28 + 4.57 \ln X$	0.80
Planaxis planicostata	24	$Y = -4.44 + 1.86 \ln X$	0.91
Acanthina brevidentata	24	$Y = -21.45 + 8.01 \ln X$	0.83
Cerithium stercusmuscarum	30	$Y = -5.54 + 2.13 \ln X$	0.80
Anachis fluctuata	26	$Y = -2.39 + 1.04 \ln X$	0.92
Nerita funiculata	37	$Y = -0.76 + 1.77 \ln X$	0.70

indicates that investment into shell material is a reasonable estimate of antipredation investment, but that other factors, such as shell architecture, are also important.

In addition to having a relatively heavy shell, *A. fluctuata* has a narrow aperture (Fig. 1) which has been suggested to reduce predation by crabs (Vermeij, 1978; Zipser & Vermeij, 1978). A narrow aperture reduces the effectiveness of shell peeling predation by not permitting a predator to insert its dactyl molar in the aperture of the shell, forcing breakage using the crushing technique, which is only effective on smaller shells. This is evident in the breakage found on *A. fluctuata* when compared to *Planaxis planicostata*, which is a similarly heavy shell with a wider aperture (Fig. 1). While only 12% of the *Anachis fluctuata* shells broken in the laboratory tests were peeled, 92% of the *Planaxis planicostata* were peeled.

Results of critical shell size tests on *Acanthina brevidentata* and *Cantharus ringens*, two common larger gastropod species, using *Ozius* predators are presented in Table V. Significantly larger *Acanthina brevidentata* shells, both in terms of shell

TABLE V

Ozius verreauxii predation on *Acanthina brevidentata*, *Cantharus ringens*, and *Cantharus ringens* with its varices artificially removed.

Predator and prey	Largest crushed (mm)	Largest peeled (mm)	Shell weight of largest taken (g)	Flesh weight of largest taken (g)
51.1 mm male				
Acanthina (hermited)	–	32.2	6.36	0.261
Cantharus (hermited)	20.1	30.0	3.26	0.160
Cantharus (varices removed)	–	31.0	–	–
Acanthina (live)	–	32.5	–	–
42.7 mm male				
Acanthina (hermited)	19.1	25.4	4.46	0.156
Cantharus (hermited)	–	23.5	2.14	0.096
Cantharus (varices removed)	–	28.0	–	–
Acanthina (live)	–	24.5	–	–
49.4 mm female				
Acanthina (hermited)	22.7	27.1	4.97	0.182
Cantharus (hermited)	–	25.4	2.50	0.115
Cantharus (varices removed)	–	29.0	–	–
Acanthina (live)	22.2	27.0	–	–
53.5 mm female				
Acanthina (hermited)	–	28.2	5.29	0.199
Cantharus (hermited)	–	27.7	2.89	0.137
Cantharus (varices removed)	–	29.8	–	–
Acanthina (live)	–	30.0	–	–
40.0 mm female				
Acanthina (hermited)	–	21.5	3.15	0.095
Cantharus (hermited)	–	20.5	1.52	0.067
Cantharus (varices removed)	–	21.5	–	–
Acanthina (live)	–	20.9	–	–

TABLE V (continued)

Predator and prey	Largest crushed (mm)	Largest peeled (mm)	Shell weight of largest taken (g)	Flesh weight of largest taken (g)
41.5 mm female				
Acanthina (hermited)	–	26.1	4.66	0.166
Cantharus (hermited)	–	25.3	2.48	0.114
Cantharus (varices removed)		27.5	–	
Acanthina (live)	–	26.0		
48.9 mm male				
Acanthina (hermited)	18.2	21.8	3.23	0.100
Cantharus (hermited)	–	21.2	1.67	0.074
Cantharus (varices removed)	–	27.9	–	
Acanthina (live)	–	22.2	–	
50.0 mm male				
Acanthina (hermited)	–	25.1	4.36	0.151
Cantharus (hermited)	–	23.5	2.14	0.096
Cantharus (varices removed)	–	28.4		
Acanthina (live)	–	24.5	–	–
54.8 mm female				
Acanthina (hermited)	19.4	22.7	3.56	0.114
Cantharus (hermited)		21.7	1.78	0.079
Cantharus (varices removed)	–	30.1	–	
Acanthina (live)	–	23.1	–	–
48.0 mm female				
Acanthina (hermited)	–	22.7	3.56	0.114
Cantharus (hermited)	–	23.5	2.14	0.096
Cantharus (varices removed)	–	26.2		

weight and gastropod flesh weight, were successfully preyed upon than *Cantharus ringens* shells ($P < 0.01$, paired t-test). This result would not be expected considering the shell weight to internal volume relations of these shell-types, since *Acanthina brevidentata* has a significantly heavier shell than *Cantharus ringens* of similar volume and columellar length (Bertness, 1980b). *C. ringens*, however, has large terminal axial varices which have been suggested to protect gastropods from peeling predation (Vermeij, 1978). To examine the functional significance of this architectural feature, critical shell size tests were made with *C. ringens* shells on which the terminal varices had been artificially removed (see p. 215). Results of these tests (Table V) show that removal of the axial varices significantly increased the critical shell size necessary to escape predation by *Ozius* ($P < 0.01$, paired t-test).

The critical sizes of live *Acanthina brevidentata* to the laboratory *Ozius* are also given in Table V. There was no significant difference between the critical size of live *Acanthina brevidentata* and *A. brevidentata* shells occupied by hermit crabs ($P > 0.05$, paired t-test). This indicates that the type of organism inhabiting a shell did not affect the vulnerability of the shell to decapod predators. In addition, in tests designed to determine whether crab predators had a preference for either live snails or snail shells occupied by hermit crabs, both *Ozius* ($P > 0.05$, $n = 38$, χ^2) and *Eriphia* ($P > 0.05$, $n = 25$, χ^2) showed no significant preference.

FIELD SHELL INJURY DATA

Shells are in extremely short supply for hermit crabs in the Bay of Panama and they are found inhabiting even the most severely damaged shells (Bertness, 1980a). This makes the assessment of the relative frequency of predation on different shell types possible, since hermit crabs essentially pick up a random sample of empty gastropod shells that can be examined for predator damage. Data on the frequency of shell damage from shells found occupied by hermit crabs at two sites in the Bay of Panama are given in Table VI. Since similar patterns of damage were found at the two locations, shell-type comparisons were made on the combined data (Table VI).

TABLE VI

Data on the frequency of predator inflicted shell damage on shells found occupied by hermit crabs on Culebra and Flamenco Islands, Panama.

	Culebra Island		Flamenco Island		Combined samples	
Gastropod species	*n*	% injured	*n*	% injured	*n*	% injured
Nerita funiculata	248	6	86	0	334	5.0
Planaxis planicostata	44	25	356	12	400	14
Anachis fluctuata	35	3	23	0	58	2
Cerithium stercusmuscarum	45	43	52	69	97	57
Acanthina brevidentata	31	35	17	18	48	29
Cantharus ringens	56	20	67	9	123	14

Examining the four smaller shell-types studied in the laboratory predation tests (Tables I and II), *Cerithium stercusmuscarum* was found injured significantly more than the other three shell types ($P < 0.001$, χ^2); *Planaxis planicostata* was found damaged significantly more than either *Anachis fluctuata* or *Nerita funiculata* ($P < 0.05$, χ^2); while there was no significant difference in the proportion of *Anachis fluctuata* and *Nerita funiculata* shells found injured ($P > 0.05$, χ^2). Since *N. funiculata* was found in the laboratory tests to be the most vulnerable shell to crab predators, the low frequency of damaged nerite shells in the natural habitat is anomalous. This would appear to be due to the fact that shell breakage on *N. funiculata* renders them unsuitable for hermit crab occupation and therefore damaged nerite shells are underrepresented in the shells utilized by hermit crabs (Bertness, 1980a). The general pattern of shell damage on shells occupied by hermit crabs then supports the laboratory findings that shell vulnerability to shell breaking predators increases in the order *Anachis fluctuata* > *Planaxis planicostata* > *Cerithium stercusmuscarum* > *Nerita funiculata* for these smaller shells.

Of the two larger shell types examined in the laboratory *Acanthina brevidentata* was found damaged significantly more than *Cantharus ringens* ($P < 0.01$, χ^2). These results support the laboratory finding that *Acanthina brevidentata* is more vulnerable to crab predators than *Cantharus ringens*.

DISCUSSION

Both crab predators examined in this paper exhibited similar shell breaking behavior. Small shells relative to a given crab's body size were crushed by progressively breaking off the apex of the shell until the occupant of the shell could be removed. Larger shells, close to the largest shell a given predator was able to break, were peeled by progressively chipping away the lip of the shell until the occupant could be removed. Both of these shell breaking methods have been described in other tropical and subtropical crab species (Shoup, 1968; Rossi & Parisi, 1973; Vermeij, 1976, 1978; Zipser & Vermeij, 1978), and Zipser & Vermeij (1978) suggested the size effect on the utilization of these breakage techniques in Guamanian crabs.

Vermeij (1978) suggested that apex-breaking is a very commonly employed method of shell-breaking in tropical crab predators, while the shell-peeling technique is especially characteristic of *Calappa* spp. and spiny lobsters which are morphologically adapted for peeling away the lip of shells (Shoup, 1968; Kent, 1979). Our results suggest that morphological adaptations that allow tropical crabs to peel shells are more common than previously thought. The large dactyl molars of both *Ozius* and *Eriphia* (Fig. 2) are well suited for breaking shells using either a crushing or peeling technique. Large molariform teeth located on the inside proximal edge of the dactylus, maximizing mechanical advantage, appear to be common in tropical xanthids.

Results of the predation size refuge tests indicate that the gastropod species available to *Ozius* and *Eriphia* as prey items vary significantly in their vulnerability to shell breaking crabs. These differences are reflected in the frequency of damage on shells in the natural habitat. Gastropods that invest more into shell material are generally better protected from predators than species that have lighter shells. Shell architecture is also an important determinant of a shell's susceptibility to shell crushing predation. Narrow apertures, as in *Anachis fluctuata*, prevent crab predators from effectively using the peeling technique, by not allowing a crab to insert its dactyl molar into the aperture to initiate peeling. Strong axial sculpture, as illustrated in the large terminal varices of *Cantharus ringens*, also deters crab predation. Terminal varices strengthen the lip of the shell, which reduces the risk of peeling predation. Thickened shells, narrow apertures, and shell sculpture have all been previously suggested to reduce the predation risk of gastropods (see Vermeij, 1978, for review) and appear to be coevolved traits designed by natural selection to deter predation.

Close sympatry between crab shell predators and their gastropod prey appears to be enforced by fish predation in the Bay of Panama. Large *Diodon* spp. (spiny puffers), *Arothron* spp. (smooth puffers), and *Scarus* spp. (parrot fish) forage in the intertidal habitat during high tide feeding on gastropods and decapods (unpubl. data; Menge, pers. comm.). The most common fish predator, *Diodon hystrix*, is large and capable of crushing all but the largest intertidal gastropods (unpubl. data). Experimental analysis of fish predation on gastropods in the Bay of Panama showed that gastropods exposed on open surfaces at high tide suffered a 10–28% daily predation rate (Bertness, 1980c). In response to this heavy predation, crabs and snails on rocky shores in the Bay of Panama retreat to crevices and under rocks during high tide. This close sympatry between crab predators and their gastropod prey appears to have led to the coevolution of efficiently designed crushing claws in the predators and antipredation shell architecture in the gastropods. Larger gastropods (e.g. *Muricanthus radix*, *Thais kioskiformis*, and *Cymia tecta*) often live in the open exposed to fish predators. These snails are too large for most crustacean predators to damage and they do not show a high incidence of architectural features which deter crab predators, such as narrow apertures and axial shell sculpture. The most common architectural characteristics on larger shells which are often exposed to fish predators are stout spines or nodes on the periphery of the shell which have been demonstrated to reduce the efficiency of fish predators (Palmer, 1979).

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